BULLETIN OF MARINE SCIENCE, 46(3): 677–687, 1990

GROWTH, MORTALITY, REPRODUCTION AND FEEDING OF KNOBBED PORGY, *CALAMUS NODOSUS,* ALONG THE SOUTHEASTERN UNITED STATES COAST

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ABSTRACT

We studied age, growth, mortality, age/size composition, reproduction and feeding of knobbed porgy caught off North Carolina and South Carolina from 1972 to 1978. Maximum age determined from scales was 17 years for a 460 mm TL specimen. Annual increments in back-calculated length were 194 mm the first year, 57 mm the second year, and 42, 34 and 25 mm for years 3–5. Annual growth for ages 6–10 and 11–16 years averaged 13 and 12 mm. The von Bertalanffy growth model fitted to these data was $L = 512$ mm $(1 - e^{-0.174(t+0.878)})$. Observed lengths at age for hook and line were significantly larger ($P < 0.05$) than trawl caught specimens by about 40 mm on average. Knobbed porgy were fully recruited to the recreational fishery at age 10 years (13.5% of the catch). Partial recruitment was gradual; ages 4–7 and 8 and 9 years made up 33 and 34% of the catch. Following full recruitment, ages 11–17 years accounted for only 15% of the catch. In contrast, knobbed porgy were fully vulnerable to the trawl at 7 years. Instantaneous mortality rates (Z) ranged from 0.526–0.742. Sex ratio at size and age data indicated that knobbed porgy are protogynous hermaphrodites, changing sex when they are 300–500 mm TL. Females were significantly predominant in the sample population (59%). Monthly mean gonosomatic indices suggest that fish spawn in May and June. Limited diet data showed that knobbed porgy are benthic carnivores preying primarily on mollusks, crabs, polychaetes and sea urchins, which they crush with their strong jaw and pharyngeal teeth.

Catches of the knobbed porgy, *Calamus nodosus* (Sparidae) contribute significantly to recreational and commercial catches of reef fish off the southeastern U.S. coast. Headboats fishing the middle and outer continental shelf off North Carolina and South Carolina from 1972 to 1977 landed 590–527 metric tons (mt) (1.3–1.6 million pounds) of reef fishes annually (exclusive of black seabass, *Centropristis striata*). Collectively porgies (including *Pagrus pagrus, C. leucosteus, C. nodosus, C. bajonado* and *C. proridens*) accounted for over 50% of the catch in numbers (Huntsman unpublished data). Recreational catches of porgies (including the above species and *Diplodus argenteus* and *Stenotomus caprinus*) in the entire U.S. South Atlantic Bight in 1986 and 1987 were estimated to be 92,000 and 57,000 fish, respectively (NMFS, 1987, in press). In 1986 and 1987 commercial catches of all the above porgies from North Carolina, South Carolina and Georgia were 40 and 34 mt (100,300 and 75,600 pounds), respectively (NMFS, unpublished data).

Knobbed porgy occur at depths of 11 to 84 m (6–46 fm) from North Carolina to Campeche Banks, Mexico (Randall and Caldwell, 1966). Off North Carolina and South Carolina they are associated with wrecks, reefs and rock outcroppings along the outer continental shelf (Struhsaker, 1969; Powles and Barans, 1980; Grimes et al., 1982; Sedberry and Van Dolah, 1984) and are occasionally taken over predominantly sandy bottoms (Wenner et al., 1980). The purpose of this paper is to report on age, growth, mortality, reproductive biology, diet and age/size composition of knobbed porgy from the recreational fishery off North Carolina and South Carolina.

Materials and Methods

Most biological samples were obtained from the hook-and-line recreational headboat catch off North Carolina and South Carolina. Some fish were also collected by hook and line from the NMFS R/V Onslow Bay and by 2-cm (0.75 in) stretched-mesh "Yankee trawl" from the R/V Dolphin (South Carolina Wildlife and Marine Resources Department).

Standard procedures were followed in the field and laboratory. Fish were sexed (apparent sex by visual inspection), measured (TL in mm), weighed (nearest 45 g) and aging structures (scales and some sagittal otoliths) were removed. Sex information was not always obtained with scale samples that were collected during brief dockside intercepts of anglers. Scales were removed from below the left pectoral fin, mounted between glass slides and observed with a binocular dissecting microscope. Measurements for back-calculation of lengths-at-age were made from the scale focus to each annulus and the anterior-lateral margin (scale edge) using an ocular micrometer. Sagittae were stored dry or in glycerin and examined whole while immersed in clove oil using reflected light against a dark background.

We determined the size structure of knobbed porgies in the recreational fishery by randomly measuring headboat catches at dockside. We constructed an age/length key to convert length frequencies to age frequencies and construct a catch curve to estimate instantaneous total mortality (Z) (Ricker, 1975). Because of small sample sizes we pooled data collected from 1972 to 1978 for age, growth, age structure and mortality analyses, recognizing that the effects of annual recruitment variation would be obscured (Ricker, 1975).

Gastrointestinal tracts and gonads were removed from fish collected on the R/V Onslow Bay and some recreational fishery samples, preserved in 10% formalin and later stored in 70% isopropyl alcohol. Gonads were removed from preservative and weighed (nearest 0.1 g) after surface moisture was absorbed by blotting.

We used a gonosomatic index to determine reproductive seasonality (Nikolsky, 1963). The index was calculated as GI = GW/BW, where GW was preserved gonad weight (g) and BW was body weight (g).

Guts were dissected and the contents examined using a binocular dissecting microscope. Foods were identified to the most precise taxonomic level possible, and their frequency of occurrence in stomachs was recorded.

Results

Age and Growth.—From 1972 to 1978, scales from 753 fish were collected from the hook-and-line fishery. Fish with observable annuli (399 or 53%) ranged from 240–513 mm TL. We examined scales from trawl caught fish and were able to observe annuli on 74 fish ranging from 273–476 mm TL. Annuli were recognized as closely spaced circuli and/or circuli displaying marked crossing over in the anterior-lateral field. Otoliths (23) had successive hyaline and opaque bands. By observing otoliths from specimens collected throughout the year we determined that the narrower hyaline band represented winter-spring growth. Hyaline bands gradually merged with broader opaque bands which formed during summer-fall growth. The beginning of the opaque zone was designated as the annulus.

We were not able to establish directly that scale rings were deposited annually; however, the following evidence is consistent with that hypothesis. The frequency distribution of annulus measurements (scale foci to annuli) showed that each annulus was represented by a single mode, and the modes were consistent for successively larger (older) fish (Fig. 1). There was increasing overlap in measurement distributions for larger (older) fish with more annuli, and the distance between modes became smaller for larger (older) fish with more annuli. Scale growth and fish growth were proportional and curvilinearly related by the equation $TL = 19.54SR^{0.7279}$ (TL = total length, mm; SR = scale radius, ocular micrometer units; $r = 0.81$ and $N = 399$). Back-calculated lengths agreed reasonably well with mean lengths at capture for the same inferred ages, particularly for the younger ages.

Evidently, otolith bands were also deposited annually. By observing otoliths from fish collected throughout the year we determined that the opaque growth

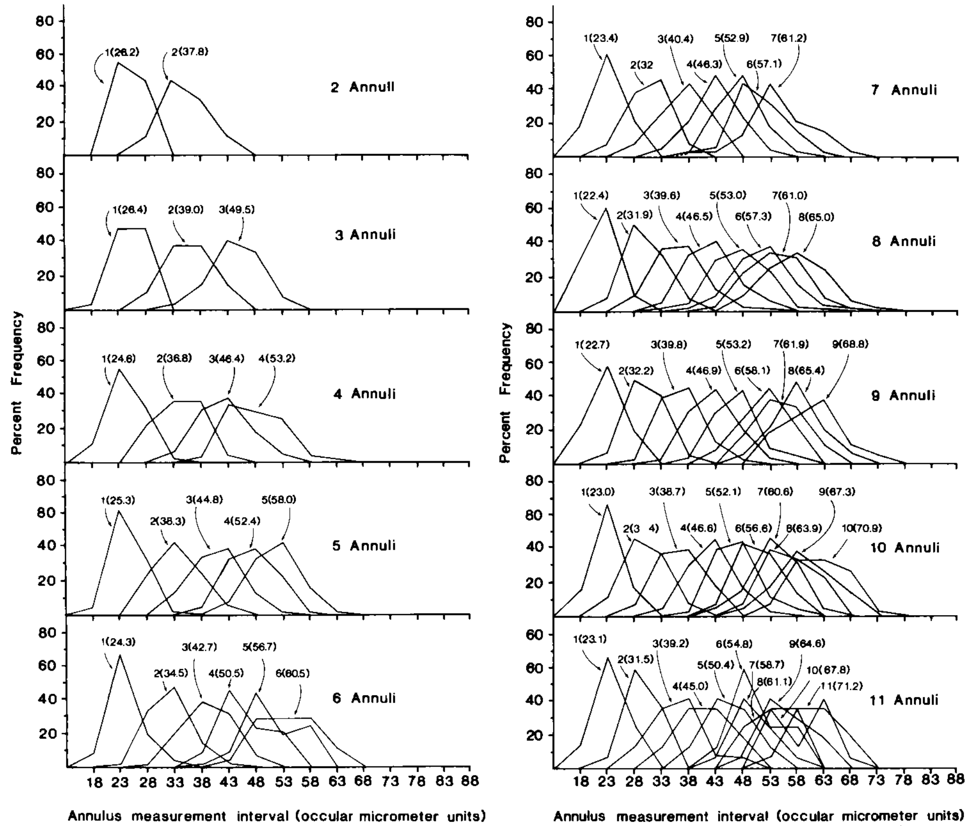

Figure 1. Frequency distribution of measurements from scale foci to each annulus grouped by the number of annuli on scales. Mean values for each annulus group are in parentheses.

zone (its beginning or inside edge designated the annulus) was initiated in June and July. Because observed mean lengths at inferred ages were similar for scale and otolith-aged fish (Table 1), annulus formation on scales also occurred in early summer. Attempts to verify this timing by marginal scale increment analysis were inconclusive.

We did not rigorously evaluate the precision of our aging, but indirect evidence suggests it was marginally adequate. Ages agreed in 8 of 23 paired comparisons of scales and otoliths, and an additional 12 comparisons agreed to within one year (i.e., 20 of 23 comparisons or 87% agreed within 1 year). Observed mean lengths at capture for scale-aged and otolith-aged fish were similar; however, mean sizes of otolith-aged fish were larger than scale-aged for the first six annuli (Table 1). This discrepancy probably occurred because scale annuli were recognizable before otolith annuli. For annuli 7–10 observed mean lengths were inconsistent between scale-aged and otolith-aged animals (Table 1), no doubt owing to increasing difficulty in reading both structures in older fish.

The maximum longevity we observed was 17 years for a 460 mm TL individual. The largest fish observed was 544 mm TL of unknown age. The oldest fish (17 yr) was caught in the recreational fishery, while the oldest trawl caught specimen was age 11 at 431 mm TL.

Table 1. Back-calculated, annual increments and observed mean lengths-at-scale age (years) and observed mean length at otolith age (years) for knobbed porgy collected by hook and line from 1972–1978

Age (yr)	N	Annulus 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	0																	
2	8	206	270															
3	18	207	277	326														
4	43	202	268	318	352													
5	47	202	263	308	345	371												
6	38	197	258	299	335	363	383											
7	34	190	242	287	324	351	372	391										
8	57	188	247	285	320	351	371	389	407									
9	67	191	242	285	320	351	374	391	408	423								
10	43	192	242	284	320	348	371	389	405	420	437							
11	15	187	235	274	303	331	351	369	383	397	412	428						
12	10	183	232	275	306	333	358	375	389	404	418	431	441					
13	12	184	229	264	299	329	353	369	385	398	411	426	441	457				
14	3	179	221	258	284	329	348	370	386	397	408	423	435	449	461			
15	1	203	255	297	352	371	394	412	422	448	461	474	492	513	525	538		
16	2	179	229	260	297	325	350	366	387	399	412	427	438	446	455	464	470	
17	1	179	238	297	332	356	375	385	394	399	412	431	439	457	461	470	487	504
weighted mean back-calculated																		
		194	251	293	327	352	371	384	403	416	425	429	442	458	468	484	476	504
annual increments in back-calculated																		
		194	57	42	34	25	19	13	19	13	9	4	13	16	10	16	—	—
observed mean-scale aged																		
			283	321	349	365	389	410	432	440	461	457	465	470	472	481	482	460
observed mean-otolith aged																		
			295	322	376	390	418	395	450	441	448							
N =			2	6	7	10	6	1	5	4	4							

Table 2. Von Bertalanffy growth parameters for knobbed porgy and co-occurring species in the headboat fishery, and the comparative growth parameter ω (Gallucci and Quinn, 1979)

Species (Reference)	K	L	ω (=K·L_∞)	Maximum age
Rhomboplites aurorubens (Grimes, 1978)	0.198	626	123.9	10
Lutjanus campechanus (Nelson and Manooch, 1982)	0.16	975	156	16
Haemulon plumieri (Manooch, 1977)	0.108	640	69.1	13
H. aurolineatum (Manooch and Barans, 1982)	0.22	310	68.2	9
Mycteroperca microlepis (Manooch and Haimovici, 1978)	0.121	1,290	156.1	13
M. phenax (Matheson et al., 1986)	0.092	985	90.6	21
Epinephelus neviatus (Matheson and Huntsman, 1984)	0.074	1,255	92.9	25
E. drummondhayi (Matheson and Huntsman, 1984)	0.13	967	125.7	25
Pagrus pagrus (Manooch and Huntsman, 1977)	0.096	763	73.2	15
Calamus leucosteus (Waltz et al., 1982)	0.233	368	85.7	12
Calamus nodosus (this study)	0.174	512	89.08	17

We used the regression equation of TL on scale radius to back-calculate length at each annulus (Table 1). Growth was rapid the first 4 or 5 years of life (averaged 82 mm) then slowed markedly with increasing age (annual growth years 6 to 10 averaged 13 mm and years 11 to 16 averaged 12 mm). "Rosa Lee's phenomenon" or increasingly smaller calculated lengths for older fish is apparent in the data (Table 1).

We fitted the von Bertalanffy (1938) growth model to weighted mean back-calculated lengths (Table 1) using nonlinear regression (Helwig and Council, 1979). The equation was $L_t = 512$ mm $(1 - e^{-0.174(t+0.878)})$, where L_t is total length in mm and t is time in years. The calculated asymptotic length (L_∞) of 512 mm, although slightly conservative, agrees well with the maximum observed length of 544 mm.

Knobbed porgy are slower growing than most other reef fishes (Table 2) that co-occur in the headboat fishery. Because von Bertalanffy parameters L (maximum theoretical length) and K (growth coefficient) are inversely correlated (Knight, 1968), comparisons among species should not be made unless fitted ages are equal. Therefore, we used the growth parameter ω (=K·L_∞) suggested by Gallucci and Quinn (1979) to make rough comparisons. Knobbed porgy growth was most similar to its congener the whitebone porgy, *Calamus leucosteus,* and the red porgy, *Pagrus pagrus,* but faster than the grunts, *Haemulon plumieri* and *H. aurolineatum* (Table 2).

We compared the growth of hook-and-line and trawl-caught fish. Observed length at age was greater by an average difference of about 40 mm for hook-and-line-caught fish for all ages except age 2 (Fig. 2). ANOVA indicated that lengths at age were significantly different ($P < 0.05$) for the comparable ages 2–11 years.

The length-weight relationship of 915 knobbed porgy ranging in size from 240 to 544 mm TL was $W = 7.65 \times 10^{-9} TL^{3.13}$ ($r = 0.974$, W in kg and TL in mm).

Age Structure and Mortality.—We used an age-length key constructed with ages for all years and randomly measured lengths (N = 944) to estimate the age structure of the recreational headboat fishery from 1972 to 1978. The age of full recruitment to the recreational fishery was 10 years, and all younger ages except one year were partially recruited (Fig. 3). Ages 4 to 9 comprised 67% of the fishery and, following recruitment, older ages (11–17) accounted for only 15%.

The small sample of 74 fish collected by trawl had a younger age structure than

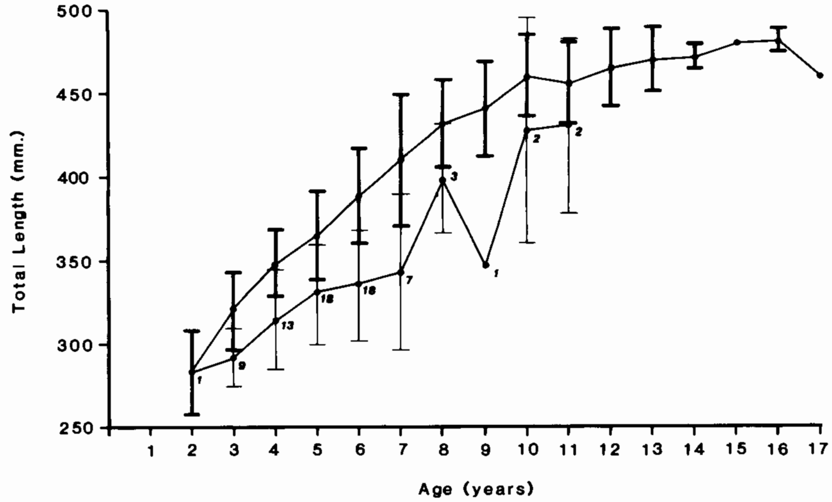

Figure 2. Mean empirical length at age of knobbed porgy determined from scale samples collected by hook and line (upper line) and trawl (lower line). Sample sizes for trawl-caught fish are shown (see Table 1 for hook-and-line-sample sizes), and error bars indicate two standard deviations about the mean.

the recreational catch. Fish were fully recruited at age 7 years (343 mm mean observed TL), and that age group accounted for 9% of the catch. Partially recruited ages 2–6 years made up 80% of the catch, while ages 8–11 years accounted for 9.5%.

We estimated total instantaneous mortality (Z) for the recreational fishery, as the slope of the linear regression of loge frequency on age for ages 10 to 17 years and by the methods of Jackson, Heinke, and Robson and Chapman (Everhardt and Youngs, 1981). Instantaneous rates (Z) were converted to total annual mortality rates (A) using the relationship $A = 1 - e^{-Z}$. The estimates were:

Method	Z	A
Regression	0.526	0.409
Jackson	0.656	0.481
Heinke	0.669	0.488
Robson and Chapman	0.742	0.524

Reproduction.—The apparent sex of 143 knobbed porgy (85 females and 58 males) was determined by visual inspection. We examined fish collected May through November when gonads were well developed, making apparent sex obvious. Ovaries were rose to reddish elongate sacks containing ovigerous lamellae and a central lumen; testes were also elongate, but solid, smooth, lobed and creamy white. Ovotestes were never observed.

Although sex ratio for the entire sample population was not significantly variant from 1:1 (1.5 ♀♀ : 1 ♂♂ or 59% ♀♀ : 41% ♂♂; $\chi^2 = 2.36$, $\chi^2_{0.05} = 3.84$; N = 143), when combined with age and size information the sex distribution is disparate and therefore suggests that knobbed porgy are protogynous hermaphrodites (Figs. 4, 5). Females predominated at size intervals <441 mm TL (accounting for 88% of all fish <441 mm TL), and males were preponderant above 441 mm TL (accounting for 72% of all fish >441 mm TL). There were two exceptions to this

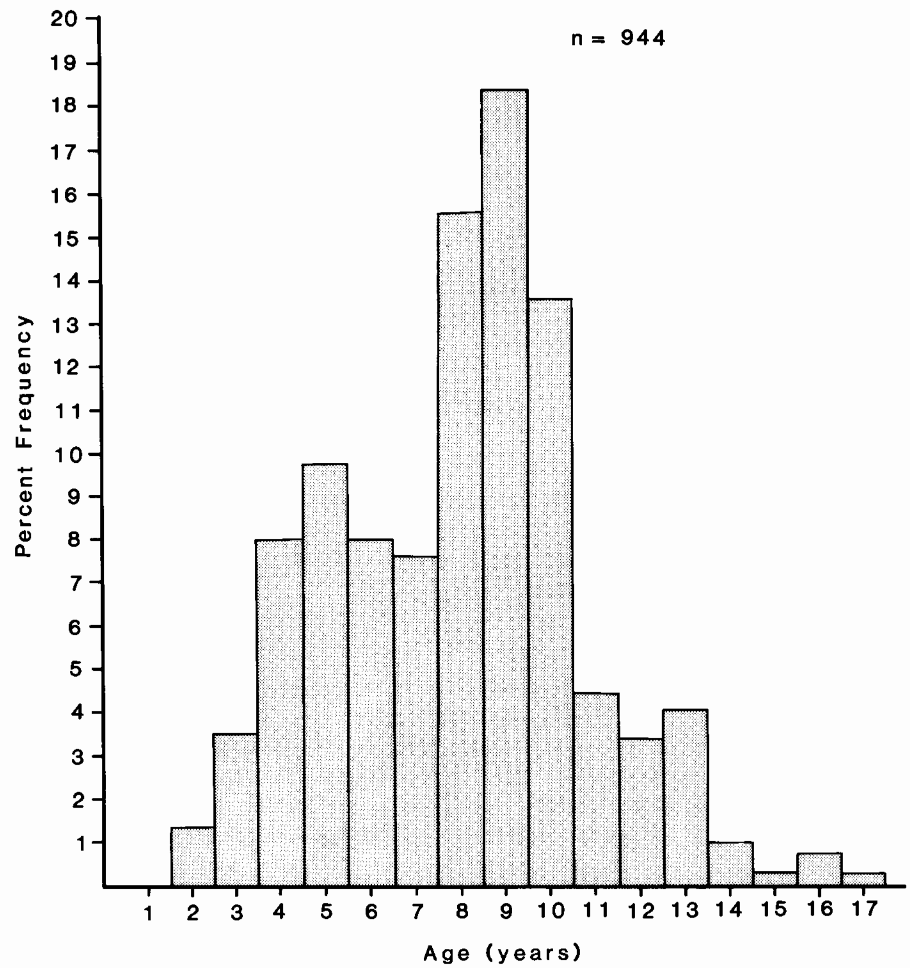

Figure 3. Age structure of knobbed porgy in the headboat fishery off North Carolina and South Carolina 1972 to 1978.

trend; one male occurred in the 221–240 mm TL interval, and one female occurred in the 541–560 mm TL interval (Fig. 4). Between the ages 1 and 7 years no males were present, and only one female (of 25 fish) was observed between ages 8 and 11 years (Fig. 4B). We used chi-square contingency tests to determine if sex ratio, and size and age were independent. Results indicated that sex ratio and size were not independent ($\chi^2 = 33.3$, $\chi^2_{0.01} = 29.1$, 14 df), however, independence of sex ratio and age was not rejected ($\chi^2 = 11.66$, $\chi^2_{0.01} = 16.9$, 9 df).

Although gonads were only collected from fish from May to November, monthly mean gonosomatic indices for both males and females indicated that spawning occurred during May and June (Fig. 5).

Foods and Feeding.—Contents of gastrointestinal tracts of 70 knobbed porgy implied that they are opportunistic benthic carnivores, preying primarily on invertebrates whose hard parts they crush with their strong jaw (molariform) and pharyngeal teeth. Due to the crushing, foods were often difficult to identify and meaningful numerical, volumetric or gravimetric quantitative analysis was im-

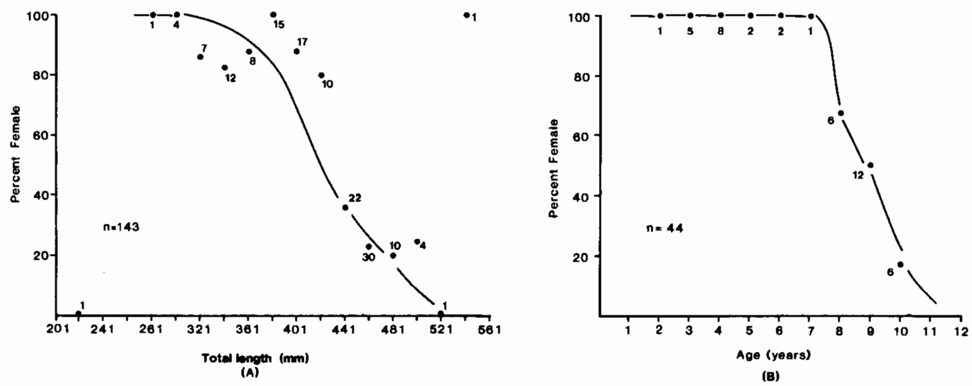

Figure 4. Sex ratio of knobbed porgy at (A) size (20 mm TL intervals) and (B) age. Sample size is indicated for each data point.

possible. However, we were able to determine frequency of occurrence by general food categories (Fig. 6). Mollusks, crabs and polychaetes were the major foods, occurring in at least 50% of the stomachs, and sea urchins, starfish and barnacles occurred in about 20% of fish examined.

Discussion

Growth.—Back-calculated lengths-at-age clearly showed that calculated lengths for any given age were smaller for older fish. This may have been the result of the differential imposition of recreational fishing mortality on the larger and faster growing members of a cohort (Ricker, 1975). The relatively large 6/0 and 7/0 hooks commonly used in the recreational fishery could account for this selective mortality on the larger fish of a given cohort. That knobbed porgy were not fully

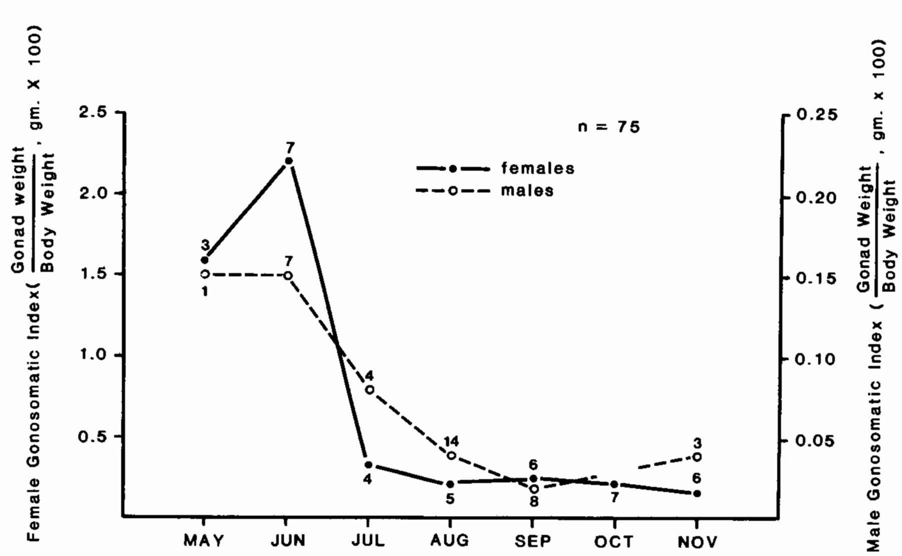

Figure 5. Monthly mean gonosomatic indices for female and male knobbed porgy.

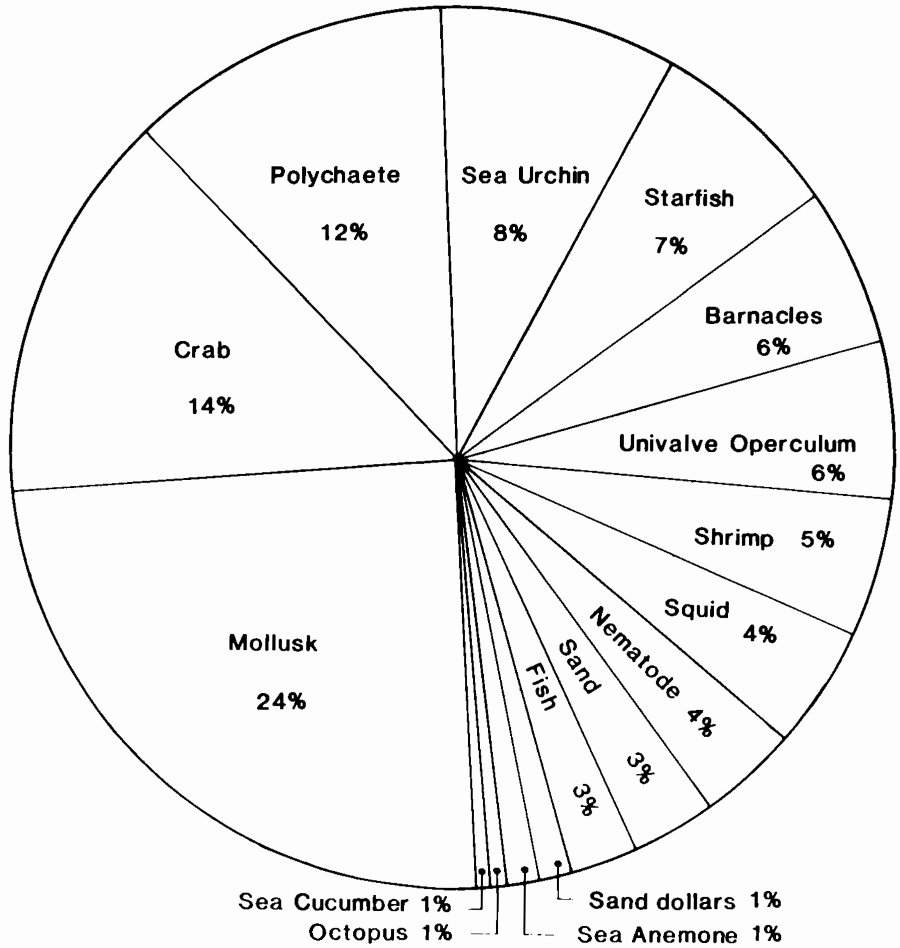

Figure 6. Percent frequency of occurrence of various foods in the diet of knobbed porgy.

recruited to the recreational fishery until age 10 years also indicated size selectivity related to fishing gear.

The comparison of observed length-at-age of trawl-caught and hook-and-line-caught fish indicated that lengths for hook-and-line-caught fish were consistently the largest. The size differences are most likely due to fishing gear selectivity creating sampling bias. Trawls probably selected for smaller fish of a given age (especially for older ages), and hook-and-line gear selected for larger fish at age.

Recruitment and Mortality.—Knobbed porgy recruit to the recreational fishery at an older age (10 years) than other frequently caught species (Table 3), and fish were recruited to the trawl fishery 3 years younger (age 7 years) than to the recreational fishery. The recruitment age for the headboat fishery was 59% of the oldest age in the fishery, the highest percentage for all species in the fishery except for *Mycteroperca phenax* which ranged from 48–62% (Tables 2, 3). Conditional mortality rates over the period from 1972–1978 were most similar to co-occurring species with similar longevity (i.e., snappers, grunts and other porgies), but greater than the longer lived groupers (Tables 2, 3).

Table 3. Annual conditional mortality (A) and age of full recruitment to the headboat fishery for knobbed porgy and co-occurring species

Species	A (%)	Recruitment age (yr)	Reference
Lutjanus campechanus	32–34	6	Nelson and Manooch, 1982
Rhomboplites aurorubens	49	4	Huntsman et al., 1983
Haemulon aurolineatum	59	5	Manooch and Barans, 1982
Haemulon plumieri	37–51	7	Manooch, 1978
Epinephelus drummondhayi	23–33	3–5	Matheson and Huntsman, 1984
E. neviatus	14–43	5–9	Matheson and Huntsman, 1984
Mycteroperca phenax	25–38	10–13	Matheson et al., 1986
Pagrus pagrus	32–55	5	Manooch and Huntsman, 1977
Calamus nodosus	41–52	10	This study

Reproduction.—Apparent sex ratios at size and age suggested that knobbed porgy are protogynous hermaphrodites, most fish beginning life as females, changing to males over a wide size range (about 300–500 mm TL), although most sex change probably occurs around 400–450 mm TL (Fig. 5). We found one male <281 mm TL and one female >540 mm TL, indicating that not all fish change sex. Waltz et al. (1982) concluded from histological evidence that the congeneric whitebone porgy was protogynous, and that only 60% of the population changed sex; the remaining 20% males and 20% females did not change sex.

Differential growth rates can result in unequal sex ratios at size (Wenner, 1972). We reject sex specific growth rates as the cause of observed sex ratios, because sex ratio at age deviated from equality just as sex ratio and size did (Fig. 6). If differential growth had caused unequal sex ratio at size, sex ratio at age should be 1:1.

Gonosomatic indices indicated spawning in May and June. Peak spawning for the congeneric whitebone porgy is May (Waltz et al., 1982), and the confamilial red porgy spawns in March and April (Manooch, 1976).

Feeding.—Our results were consistent with those generally reported for sparids. Randall (1968) indicated that the genus *Calamus* was primarily carnivorous, eating mostly invertebrates such as sea urchins, crabs and mollusks. Manooch (1977) reported crustaceans, echinoderms and mollusks in 89% of red porgy he examined, and the same categories occurred in over 90% of the fish we examined. Although these data suggest that the two species have similar diets, red porgy often take large individual food items (Manooch, 1977), while knobbed porgy specialize on the more diminutive varieties within categories. Perhaps this trophic specialization reduces competition between knobbed porgy and red porgy.

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DATE ACCEPTED: May 30, 1989.

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